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ON THE MORPHOLOGICAL AND PHYSIOLOGICAL CLASSIFICATION OF THE CUTANEOUS SENSE ORGANS OF FISHES.

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IN determining the rank and meaning of any given sense organ there are three criteria to which we may appeal. (1) Doubtless the most important is direct introspective knowledge, the psychological criterion. This criterion obviously is not available to us in the study of the senses of the lower animals, where we are shut up to the remaining two. (2) Of these the most important is direct physiological experimentation. The sense organs under consideration are subjected to various types of stimuli under experimental conditions and the reactions noted — the physiological criterion. (3) The structure of the organs frequently permits of inference as to probable function, a method of small value except as controlled by other data — the anatomical criterion.

For over two centuries it has been known that the fishes possess various highly specialized sense organs in the skin, and for over half a century it has been recognized that these belong to two distinct morphological types. The problem of the morphological and physiological significance of these organs has exercised some of the ablest zoölogists during the whole of these periods without, however, any agreement having been reached. The reason for this unsatisfactory condition is not far to seek. Most of these authors have been content with inferences as to function based on studies of the structure of the organs — a perilous course at the best — and few carefully wrought out physiological experiments have been made. By the coöperation of a number of students this condition is now largely remedied and positive conclusions become possible. We shall summarize these conclusions without in this place undertaking to give the evidence for them in detail or to cite authorities, taking up first the anatomical findings which have laid the foundation historically for the physiological differentiation of these sense organs.

In the skin of fishes there are three types of sensory nerve endings belonging to the cerebro-spinal system, aside from sympathetic nerves of uncertain physiological significance. (1) there are free endings everywhere in the skin, but especially on the lips, barblets and exposed surfaces generally. (2) Sense organs in canals or pits obviously belonging to the lateral line system and termed canal organs and pit organs, or collectively nerve hillocks or neuromasts. (3) Sense organs resembling taste buds of the mouth, lying freely exposed on the surface of the skin, never sunk below the surface, and variously termed flask-shaped organs, end-buds, terminal buds, etc.

The nerves which end free, those of the first type, usually lose their medullary sheaths some distance below the skin and have sometimes been overlooked. Merkel, for instance, in his great monograph denies the presence of these endings in the skin of fishes. Recent students of nerve components have shown that the nerves of this type are anatomically distinct from those for both the other types of sense organs for their entire extent, in all cases being provided with separate ganglia and entering the brain by distinct roots. In the trunk region these "general cutaneous" nerves make up the greater part of the dorsal spinal roots and terminate in the dorsal horns; in the head they enter by the V, X and sometimes by the IX pairs of cranial nerves and all terminate in the funicular nucleus or the gray matter associated with the spinal V tract, all morphological equivalents of the dorsal horns of the spinal cord. Morphologically the general cutaneous system of nerves is a well defined unit. Physiologically its function is unquestionably in the main tactile. Practically all parts of the body are sensitive to touch and are reached by these nerves, whether they are supplied by other types of sensory nerves or not. The more acute the tactile sensibility, the more rich the innervation by fibers of this system.

The differentiation of the sense organs of the second and third types has proven very difficult, for the reason that rows of undoubted lateral line organs which are certainly homologous appear in one species as canal organs, in another as pit organs and in still another as naked sense organs, and the separation of the latter from the terminal buds of the third type is often a matter of difficulty. This has led many of the students of these organs to deny the validity of the distinction between neuromasts and terminal buds, classing both as variants of one type.

In 1870 Schulze discovered that the neuromasts, whether enclosed within canals or exposed upon the surface, are characterized by the presence of specific sensory cells, the pear cells or hair cells, which extend only part way through the sensory epithelium, while the specific sensory cells of the terminal buds, like those of taste buds, extend from the external to internal limiting membrane of the epithelium. This has been generally confirmed and receives further support and interpretation from the recent demonstration that neuromasts and terminal buds receive distinct and strictly characteristic innervation.

All neuromasts, whether canal organs, pit organs or naked organs, are innervated by fibers which are separable from all other types of nerve fibers, with separate ganglia and roots, and all of which terminate in the tuberculum acusticum or in the cerebellum. The sense organs of the internal ear have the same general structure as the neuromasts of the skin and are likewise innervated from the tuberculum acusticum, so that the whole system is termed the acustico-lateral system of nerves and sense organs. The tuberculum acusticum and its derivative, the cerebellum, are morphologically intimately related to the general cutaneous centers of the dorsal horn, and the whole acustico-lateral system is in all probability phylogenetically derived from the general cutaneous system.

This probability is strengthened by the results of recent physiological experiments upon this system. The lateral line system of fishes as a whole is undoubtedly concerned in the maintenance of bodily equilibrium, and the method of stimulation here is closely similar to that of ordinary tactile nerves, and doubtless derived from it. The function of orientation in space is especially localized in the semicircular canals of the internal ear, of like phylogenetic origin with the lateral line canals, and this part of the system persists in all terrestrial vertebrates.

Parker has also shown that the lateral line organs of fishes are sensitive to mechanical jars of low frequency. This again is closely related to the tactile function and has doubtless given rise phylogenetically to the power of perceiving rhythmic vibrations of higher frequency, viz., hearing, a part of the sense organs of the acustico-lateral system within the internal ear having been set apart for this function in the course of vertebrate evolution.

Having now a morphological criterion for defining the cutaneous sense organs belonging to the lateral line system, it may be stated briefly that all other specialized cutaneous sense organs of fishes at present known may be grouped with the taste buds of the buccal cavity both on the basis of their structure and of their innervation. The nerve supply of all of these organs is now known to be from a system of nerves distinct for their entire extent from those previously considered, but intimately related centrally to the sensory nerves from visceral surfaces in general. This is known to students of nerve components as the communis system of nerves and sense organs, because its fibers all end centrally in the gray matter connected with the fasciculus communis (= f. solitarius of human anatomy).

This system of nerves, like the acustico-lateralis, is well developed in certain cranial nerves only, and, as the latter system is supposed to have evolved from the general cutaneous system, so the communis system has probably been differentiated from the general visceral sensory nerves of the trunk. Peripherally it is easy to distinguish the unspecialized component of this system from that which is distributed to special sense organs; but centrally this is much more difficult. This, however, I think I have accomplished in part at least in the case of Ameiurus. At any rate, the chief ascending gustatory path in these fishes is clearly separable from all other reflex paths from the primary communis centers.

No important distinction can be drawn either in structure or in innervation between the terminal buds of the outer skin and the taste buds of the mouth, and to complete our argument it remains to show whether these sense organs are similar in function also. This has now been accomplished. In July, 1902, I presented before the American Association for the Advancement of Science at the Pittsburg meeting the report of certain experiments made upon the common cat fish, Ameiurus, which go to show that this animal actually tastes with the terminal buds known to be freely distributed over the body surfaces and especially on the barblets. Since that report I have extended these observations upon a number of marine fishes, particularly the gadoids, and the report upon this work is now in press in the *Bulletin of the U. S. Fish Commission.*

It may be regarded as established that fishes which possess terminal buds in the outer skin taste by means of these organs and habitually find their food by their means, while fishes which lack these organs in the skin have the sense of taste confined to the mouth. The delicacy of the sense of taste in the skin is directly proportional to the number of terminal buds in the areas in question. Numerous unrelated types of bony fishes from the siluroids to the gadoids which possess terminal buds have developed specially modified organs to carry the buds and increase their efficiency. These organs may take the form of barblets or of free filiform fin rays and the free rays of the pelvic and dorsal fins of some gadoid fishes are thus explained.

The results of this examination may be summarized in the following form :

I. Organs of the general cutaneous system. Free nerve endings distributed over the general body surface in all vertebrates. Innervation by general cutaneous nerves ; primary centers, dorsal horns of spinal cord and homologous centers of oblongata. Function, touch.

II. Organs of the acustico-lateral system. Peripheral organs, neuromasts, or special sense organs with hair cells among indifferent supporting cells, the former extending only part way through the sensory epithelium. Typically arranged in lines on various parts of the body according to a tolerably definite pattern whose details are, however, exceedingly variable. The internal ear is a specialized part of this system. Innervation by the acustico-lateralis nerves ; primary centers tuberculum acusticum and cerebellum. Neuromasts may assume one or several of the following forms in a given fish :

1. Canal organs, regularly arranged in canals lying in the dermis or dermal bones and communicating by means of pores at frequent intervals with the surrounding water. Function, perception of mechanical jars or slow irregular vibrations and the maintenance of bodily orientation. Occur in nearly all fishes.

2. Pit organs. Similar to the last, but each organ sunk in a separate pit which opens to the surface by a pore. Usually regularly arranged in lines which are closely related to the canals and which may replace the canals. Function unknown, but probably similar to the last. The pits in which these organs are placed may become very shallow or disappear altogether, the organ becoming superficial, with no apparent change otherwise. Occur in most ganoids and teleosts and sometimes (perhaps generally) in elasmobranchs.
3. Small pit organs. Similar to the last, but smaller and always in deep pits. Not arranged in definite patterns, but irregularly distributed over the skin. Known only in siluroid fishes.
4. Ampullæ. Organs similar in plan to pit organs, lying at the bottom of long slender tubes opening by pores at the surface of the skin, the pores scattered over the head, but the inner ends of the ampullæ grouped in definite clusters. Occur only in elasmobranchs. Function unknown.
5. Vesicles of Savi. Closed vesicles, found only in the torpedoes.
6. Cristæ acusticæ. Found in the semicircular canals of all vertebrates. Function equilibration (reaction to rotary movements).
7. Maculæ acusticæ. Found in the sacculus and utriculus of all vertebrates., Function equilibration (reaction to translatory movements, and static sense ?) and hearing (?).
8. Papilla acustica basilaris. The essential nervous part of the organ of Corti. Function hearing. Found only in vertebrates above the fishes.

III. Organs of the communis system. Peripheral organs are special sense organs with the specific sensory cells extending through the whole thickness of the sensory epithelium; organ generally resting on a raised papilla of the dermis. Present in the mouth of most vertebrates and in the outer skin of some ganoid and teleostean fishes. Innervation by communis nerves; primary centers gray matter associated with the fasciculus communis (f. solitarius), in fishes the vagal and facial lobes. Function taste. There are recognized two forms with no important differences other than position.

1. Taste buds, within the mouth.
2. Terminal buds, in the outer skin, often on barblets or other specialized organs for their reception.